

FORUM ARTICLE

Genetics and Ecology of Colonization and Mass Rearing of Hawaiian Fruit Flies (Diptera: Tephritidae) for Use in Sterile Insect Control Programs

STEPHEN H. SAUL & SUSAN D. McCOMBS

Department of Entomology, University of Hawaii at Manoa, Honolulu, Hawaii'i 96822, USA

ABSTRACT. It is critical to maintain the genetic, physiological and behavioral competence of colonized populations of insect species, such as fruit flies, which are reared for release in sterile insect and other genetic control programs. Selective pressures associated with the mass rearing process affect this competence, but the underlying mechanisms of genetic change are largely unknown. However, competence is often an operational goal achieved by manipulating environmental factors without possessing precise genetic knowledge of alleles and their marginal effects on the desired traits. One goal of this paper is to show that the precise genetic and statistical analysis of components that determine competence in a broad sense or fitness in the narrower ecological sense, is extremely difficult. We can get contradictory results from the different methods for estimating genetic variation in tephritid populations. We observe low levels of allozyme variation, but high levels of recessive mutants in inbred populations. We propose that genetic variability may be maintained in colonized and mass reared laboratory populations by balanced lethal systems and that the introduction of fresh genetic material may reduce, not increase, fitness. We require rigorous and precise models of directional selection in the laboratory and selective forces in the natural environment to aid our understanding of dynamic changes in courtship and mating behavior under artificial conditions. We have chosen to examine the lek model as an example of an idea whose usefulness has yet to be determined by testing and validation. The inclusion of lek forming ability in genetic models will be dependent on rigorously establishing the validity of the lek model for each tephritid species.

INTRODUCTION

The Mediterranean fruit fly, *Ceratitis capitata* (Wiedemann), Oriental fruit fly, *Bactrocera dorsalis* (Hendel), Malaysian (or solanaceous) fruit fly, *Bactrocera latifrons* (Hendel), and melon fly, *Bactrocera cucurbitae* (Coquillett) (Hardy & Foote 1989), are destructive and feared fruit pests. These species have the potential to directly damage over 200 cultivated fruits and vegetables (White & Elson-Harris 1992). Perhaps economically more important, the threat of their migration to uninfested areas is the rationale for nearly universal quarantine regulations against agricultural products from infested areas. If we could control or eliminate the threat from fruit flies to the point where direct losses are negligible and quarantine regulations are no longer necessary, we can expect improved productivity and increased agricultural diversification in infested areas. The long term goal of fruit fly control is to enhance long-term viability and competitiveness of agricultural systems in areas currently at risk.

The sterile insect technique (SIT) has been used for control of the Mediterranean fruit fly, Oriental fruit fly and melon fly. The central operation of a SIT program is the release of massive numbers of sterilized flies from colonized stocks. Success of SIT is partly dependent upon the capacity of released insects to enter the field environment and compete adequately with wild flies (Rössler 1980). They must be able to search for mates, court, and mate. This ability is a function of their genetic, physiological, and behavioral competence or fitness. Selective forces associated with the colonization and mass rearing processes affect this competence, but we are largely ignorant of the exact underlying mechanisms of genetic change. However, as a practical matter, competence can be defined as an operational goal. We can manipulate genetic and environmental factors towards this

goal without necessarily possessing complete knowledge of the genetic basis of the desired traits. We believe that increasing our understanding of genetic, physiological, and behavioral competence and the selective forces that change this competence will help ensure the success of SIT programs.

The primary goal of this paper is to further discussion and research on aspects of genetic change during colonization and mass rearing of tephritid fruit flies. A brief discussion of the ecological concept of fitness and how it applies to mass rearing will preface our discussion of genetic and ecological genetic aspects of colonization.

ECOLOGY

Concepts of Fitness

The concept of fitness has developed independently in different fields. We choose to interpret alternate formulations, e.g., Darwinian fitness (W of Sewall Wright) from population genetics in terms of its ecological components. When we speak of the fitness of some entity, we imply a probability distribution of descendants of this entity through time. The entity can be an individual or group at many levels, e.g., allele, plasmid, transposable element, species, race, deme, or population. The time period can range from a single generation to a geological time scale.

When we try to apply this theoretical concept of fitness to real populations, we face several practical problems. We find that measurements of fitness (e.g., the intrinsic rate of natural increase used by ecologists, r) are relative terms. Although the intrinsic rate of natural increase can be defined as a measure of absolute fitness (i.e., r_{\max} —the maximal physiologically possible realizable reproduction rate in some perfect environment), in practical terms this definition of fitness has no meaning outside the context of a specified environment (Vargas & Carey 1989).

A second problem is that the relative fitness ranking of a selected individual or group compared to other individuals or groups may be altered in different environments. This is one reason that measures of the heritability of certain traits (e.g., human intelligence), where groups in different environments are compared, have been often misunderstood. The best example of this dependence of relative fitness on environment is the many thousands-year-old practice of the animal or plant breeder choosing a desirable phenotype from which to breed, thereby altering its relative fitness.

In applied insect control a commonsense, informal approach to fitness is often used, treating it operationally in terms of the goals of the program (i.e., the production of flies that successfully function in sterile insect programs). Under this approach it is sufficient to know that body size measured by pupal weight is correlated in males with increased flight ability, faster and more frequent mating; and in females with increased fecundity (Bloem et al. 1990). We do not need to know the genetic basis for body size and how this interacts with rearing conditions. We only need to know which of the factors under our control, either genetic (selecting for larger pupae) or environmental (rearing conditions), can be manipulated to achieve the desired increase in pupal weight.

The precise specification of fitness as used in ecology, r , requires age-specific survival probabilities (l_x) and age-specific fecundities (m_x) of populations (i.e., life history parameters). Since fitness measurements can include evolutionary time scales the study of ecological and genetic effects on life history parameters has become a major component of current research in evolutionary biology. There is intense research on the effects of natural and man made changes in the environment on the survival and fecundity of populations—not just of species that we wish to control or eliminate, but rare and endangered species that we wish to preserve. However, it is difficult to identify the factors truly

responsible for observed life history differences (Charlesworth 1980). We must be careful when testing the predictions of life history theory by species comparisons; there may be multiple ecological differences between the species that are unknown to the investigator. Charlesworth (1980) suggests that a better method is to make comparisons between populations of the same species that have been subjected to different demographic regimes. Fruit flies may provide an excellent experimental system. In Guatemala, Mexico and Hawai'i feral populations (introduced up to 85 years earlier) are found close to mass rearing facilities in which vastly different demographic regimes have been in effect for up to several hundred generations. We could use these natural juxtapositions to study some of the most basic questions of evolutionary biology.

Relative Importance of the Different Components of Fitness

If we try to increase the fitness of a colony by selection on life history parameters we must know what the relative effects of, say, a 10% increase in fecundity is compared to a 10% increase in effective egg laying period. Cole (1954) demonstrated the overwhelming relative importance of early reproduction in increasing the intrinsic rate of increase (r) of a population. The effect of decreasing the time to first reproduction is greatest when the fecundity is high and time to sexual maturity short. When fecundity is low and maturity delayed, the relative effect of decreasing the time to first reproduction is less. A rough approximation is that at the high values of r characteristic of colonizing species absolute increases in development rates of 10% are roughly equivalent to increases in fertility of 100% (Lewontin 1965).

Measurement of Fitness

Measurement of fitness components is extremely difficult for genetic and statistical reasons (Hartl & Clark 1989). First, intralocus genetic interactions such as allelic substitutions may have pleiotropic effects at any life stage. Therefore, as a first step, one must be able to isolate the effects of these substitutions on each of the components of fitness at each life stage. Second, the effects on fitness of interlocus genetic interactions are evident in many traits that are controlled by alleles at several to many loci. We must be able to determine whether the marginal effects of a few or several genes are important. Third, practical statistical estimation of fitness components is difficult. We may have to estimate differences in fecundity or viability as small as 1% or less, but which may still be important to population growth rate. Moreover, there is high variance often observed for some traits, especially fecundity, and the very large sample sizes required to estimate small selective differences may be impractical. This is one reason that early studies of fitness, especially in *Drosophila*, tended to concentrate on viability, which usually has lower variance than fecundity.

GENETICS

Measurement of Genetic Variation in Populations of Fruit Flies

The 2 primary methods for estimating genetic variability within and among populations of tephritids are electrophoretic analyses of allozyme frequencies and gene frequencies of visible markers. Molecular methods such as restriction fragment length polymorphisms of nuclear (Haymer et al. 1992) and mitochondrial DNA (Sheppard et al. 1992.) are becoming widely used for differentiation between populations. \bar{H} (heterozygosity), calculated from electrophoretic analysis of allozyme frequencies under the Hardy-Weinberg assumptions of equally fit alleles within a large, closed, panmictic population, is the proportion of individuals in a population expected to be heterozygous at a particular locus. \bar{H} is the expected mean heterozygosity over all loci, both monomorphic and polymorphic, within a population.

Mediterranean fruit fly populations around the world are relatively depauperate for allozyme variation when compared to presumed ancestral populations in sub-Saharan Africa. These populations were started from small numbers of individuals and these bottlenecks probably account for the low heterozygosity. The highest H values are found in populations from Kenya (0.16), Reunion Island (0.15), and South Africa (0.15–167). Populations from the Mediterranean area (0.04–0.07), Brazil and Costa Rica (0.03) and Hawai'i (0.034) showed little variability (Morgante et al. 1981, Kouri et al. 1985, Mukama 1985, Huettel et al. 1980). Huettel et al. (1980) described U-shaped vs. bimodal distributions (which would be evidence for the size of founder populations) for heterozygosity in the Mediterranean fruit fly. Unfortunately, this much cited abstract presents only conclusions and there is no data or detailed information about sampling procedures. Sampling is a critical step in analyzing natural populations and from this abstract we cannot tell whether the samples, described as large in numbers of individuals, represent an adequate number of cohorts.

The conclusion from electrophoretic analyses that populations of fruit flies are genetically depauperate is contradicted by observations that large numbers of visible mutants are segregating in long standing laboratory colonies of the Mediterranean fruit fly and *Bactrocera* Macquart species in Hawaii. High frequencies of recessive visible mutations and lethal mutations (Saul 1989, McCombs & Saul 1992a,b) are evidence that these strains contain high levels of genetic variation.

A Model of Genetic Variation

We propose a model in the Mediterranean fruit fly to account for these 2 apparently contradictory results. This model proposes that strong epistatic interactions built up over 300 or more generations of mass rearing mask the high frequency of recessives and lethals. Genetic variation is revealed only after strong inbreeding (i.e., several generations of pair matings). This is analogous to the situation in the mosquitoes *Aedes triseriatus* (Say) and *Aedes aegypti* (Linnaeus) (Matthews & Craig 1989) where it was found that strong selection under intense inbreeding favors the most heterozygous individuals. The genetic load (deaths) required to maintain heterozygosity at several independent loci each linked to lethal alleles segregating at another locus would be too great even for highly fecund species. Matthews & Craig (1989) proposed that the linkage of variants and deleterious loci to create balanced lethal systems would reduce the genetic load to tolerable levels while maintaining genetic variability. They also suggested that balanced lethal systems may be common in inbred organisms with relatively small number of chromosomes since lethal genes could be concentrated on a few chromosomes. Whether the 6 pairs of chromosomes found in tephritids, compared to the 3 in mosquitoes, qualifies as low is uncertain.

In tephritids, eye mutants and lethals may be under relatively strong negative selection pressure compared to the nearly "neutral" (Bush & Neck 1976) allozymes. We propose that the stocks contain large numbers of loci where polymorphisms are maintained by heterozygote advantage at single loci or, perhaps coadapted chromosome regions. We predict that the introduction of new genetic material into mass-reared colonies will result in a decrease in fitness because of the breakdown of coadapted genetic complexes. This model contrasts with the commonsense idea that the introduction of fresh genetic material from wild populations would increase fitness by decreasing inbreeding and homozygosity. We predict that current strains of the Mediterranean fruit fly are extremely well adapted to mass rearing and most attempts to introduce fresh genetic material from the field will decrease their fitness for this purpose.

Stability of Stocks Involving Chromosomal Rearrangements

A particularly active area of research is the development of genetic sex sorting stocks

for improving the effectiveness of SIT programs used against the Mediterranean fruit fly and other tephritids. Genetic sexing stocks depend on the incorporation of pupal color (white pupae), flightless (*v* wing), or temperature sensitive mutants into Y-autosome translocations (Saul 1989, 1990). A major concern with translocation-based sexing stocks is their breakdown through recombination (Foster et al. 1980). Even a low percentage of recombination in males between the translocation break point and the selected locus could cause the breakdown of the Y^A chromosomes (Rössler 1982, 1985). Recombinant genotypes, useless for sexing, will be produced and, if favored by selection, will soon spread throughout the colony. First reports indicated that recombination would not be a serious problem (Cladera 1981, Robinson & van Heemert 1982). Later it was found that recombination in males is low in normal lines, but it is increased slightly by the presence of chromosomal rearrangements—whether the recombinant chromosome is involved in the translocation or not (Rössler 1982).

Further experience with mass rearing of translocation stocks has revealed apparent recombination values in male flies high enough to seriously affect the stability of genetic sexing colonies. For example, the white pupal sorting strain regularly breaks down (i.e., contaminant phenotypes are found to gradually increase up to 15%) (Economopoulos et al. 1990). One strategy proposed to stabilize these translocations is to suppress crossing over in the male with inversions. However, all breakdowns in translocation lines may not be due to recombination and we should consider other possibilities.

Recombination and Related Phenomena

Recombination within the translocated chromosome can explain only 1 of the 3 aberrant phenotypes (contaminants) that appear in a Y-autosome translocation stock developed using the white pupae mutant (Mazzoli & Zapater 1990). The (homozygous) white pupae phenotypes are the likely result of recombination between the translocation break point and the white pupae locus. The other 2 aberrant phenotypes are harder to explain: 1) rare recessive white pupae phenotypes that behave as if the translocation had disappeared or reverted; and 2) "false" recombinants of unknown genotype with weak pupal color expression. The latter are thought not to have a seriously impact on the stability of the stock.

Survival of Duplication/Deficiency Zygotes

Robinson (1984) and Riva (1990) described unexpected phenotypic ratios in some translocation lines involving the white pupae (*w*) locus. They postulated that the unexpected phenotypes represent survivors to the pupal stage of duplication/deficiency zygotes that had arisen in adjacent segregations from metaphase figures. A possibly analogous situation was observed in a stock containing the rosy (*ry*) gene in a Y-autosome translocation (Saul, unpubl. data). In each generation, 2–8% of the males are small, retarded in development, and have rosy eyes whereas the Y-autosome males in this stock have wild-type eyes. The rosy eye males can survive and, when mated to homozygous rosy females, produce progeny with a skewed sex ratio of 9 females to 1 male. The strain produced from this mating continues to breed true for the skewed sex ratio. As in the white pupae case, above, the most likely explanation for these males appears to be segregation of duplication/deficiency zygotes.

Transposable Elements

Mutations sometimes occur in clusters and at high frequency in fruit fly stocks that have been genetically stable for years (McCombs & Saul 1992a,b; Livadaris et al. 1990). The triggering stimulus for these episodes may be the crossing of unrelated stocks or a mutagenesis trial using formaldehyde or radiation. This high frequency of mutation and

reversion suggests that some mutations may be related to the mobilization of transposable elements. It has been our experience that the white pupal phenotype in the Mediterranean fruit fly is especially prone to occasional reversion to wild-type. We propose that the occasional breakdown of translocation stocks involving the white pupae mutant may be due to transposable element mobilization rather than to recombination. If this is the case, some proposed solutions to maintaining stock stability (i.e., multiple translocations and inversions) may be ineffective or even irrelevant.

Other Genetic Control Methods

While the sterile insect release method is the only currently operational genetic technique used for control of fruit flies, other genetic control methods have been proposed. These involve the introduction of genetically-based losses of vigor (i.e., reductions in fecundity or sterility) into wild populations. The methods for introducing this loss of vigor into the population include translocation homozygotes, conditional lethal genes, and isochromosomes (Whitten 1979).

ECOLOGICAL GENETICS

Genetic Basis of Behavioral Traits

Paths from the genotype to the phenotype for many, if not most, quantitative traits are complex and not easily amenable to detailed genetic analysis. However, we have learned from practical experience that precise identification of alleles with marginal effects on a particular behavioral trait is not a prerequisite to modifying the trait by directional selection (Sharp et al. 1983, Boller & Calkins 1984).

Successful laboratory colonization and mass rearing, which enables the wild population to eventually adapt and survive, is accompanied by strong selection on some ecological and behavioral traits. Colonization of a wild strain of the Mediterranean fruit fly is a complex process that passes through several phases: an early phase of several generations during which mating and oviposition are poor and the majority of flies leave no offspring; and a second phase of rapid increase in productivity (i.e., the "crash and recovery cycle") (Leppa et al. 1983). There may be less desirable consequences of the adaptation to mass rearing. Inbreeding and population bottlenecks may lead to loss of genetic variability and behavioral competence (e.g., normal courtship repertoire).

Persons involved with mass rearing and colonization of the Mediterranean fruit fly often mention the anecdotal "three generation rule", which suggests that one can easily and quickly select for a wide range of ecological and behavioral changes in these populations. Clearly, for such selection to be effective, there must be genetic variation for the particular trait within the base population. This implies that the Mediterranean fruit fly retains extraordinary genetic variation and/or phenotypic plasticity in closed laboratory and mass-reared populations.

Phenotypic plasticity (Stearns 1989) has become an important area of study in evolutionary biology and is relevant to the present discussion. Stearns & Koella (1986) noted that certain organisms exhibit predictable changes in phenotype with varying environmental conditions. Phenotypic plasticity in *Drosophila* is a form of density compensation whereby uncrowded organisms mature earlier, are larger and have higher lifetime fecundities than organisms reared under crowded conditions. The role of phenotypic plasticity is undetermined in tephritid biology, but may account for many of the observations made on what are assumed to be genetic differences (e.g., oviposition choice) (Prokopy et al. 1984).

Oviposition Behavior

We will use oviposition behavior to illustrate the process of selection on behavioral traits that are related to laboratory adaptation. The main difficulties during the first few generations of laboratory culture arise from the simplified laboratory environment. This environment lacks the complex patterns of leaves, trees, and fruit; light and dark; wind and sun of the natural ecosystem. Careful attention to cultural conditions for the first few generations makes it possible to keep the population going until strong directional selection towards laboratory adapted phenotypes occurs (Muñiz 1985). We have found that special emphasis must be placed on oviposition stimuli such as type of oviposition receptacle and use of fruit extract attractants (McCombs 1992).

There are a few examples of indirect genetic analysis of female oviposition choice in tephritids. Prokopy et al. (1984) studied host fruit acceptance patterns among 3 populations of Mediterranean fruit flies reared on different hosts in Hawai'i. They deduced a genetic component by default by ruling out the other possible causes (i.e., adult or larval conditioning). Papaj et al. (1989) exposed laboratory reared and wild Mediterranean fruit flies to 2 hosts and deduced a genetic basis for oviposition choice even though they acknowledge that the experiments did not control for maternal effects. It remains to be proved whether these observed phenotypic differences in learning and retention of learning regarding oviposition choice are genetically based.

Vargas (1984) found differences between screen-adapted (females oviposit through a fine mesh cloth screen) and bottle-adapted (females oviposit through small holes in plastic containers or tubes) Mediterranean fruit flies (Tanaka 1965). Saul (unpubl. data) also observed that several screen adapted mutant strains from Israel exhibited almost no change in oviposition behavior when transferred to Hawai'i even after two years of intensive selection. Females would only use plastic cups when given no choice; if screen were available, it was always preferred. Also, Rössler (pers. comm.) in Israel found that it was difficult to get bottle adapted strains from Hawai'i to oviposit using screens. These observations suggest that there is natural variation within the species for female oviposition behavior and that strong selection during adaptation to laboratory rearing may decrease genetic variation to the point where it is difficult to select for alternate behaviors. Recent evidence suggests that these observed differences in oviposition substrate behavior may also be associated with morphological changes in female aculeus width (Jones et al. 1993).

Harris et al. (1983) selected for longer and shorter periods before a male Mediterranean fruit fly begins to court and initiate copulation. They could select for slower, but not for faster, mating within an established laboratory colony. This is consistent with the model that faster mating genotypes had become fixed by strong, but probably unintended, directional selection for mating by younger males during the period of laboratory colonization.

The complex polygenic nature of genetic variation underlying apparently simple behavioral components has made precise genetic analysis extremely difficult. Nonetheless, precise genetic analysis is clearly important to optimize control programs. We lack information as to which, if any, of the behavioral and fitness traits observed in the laboratory are correlated with phenotypes that are successful in a SIT control project (Chambers et al. 1983). At present, we must reluctantly conclude that a genetic basis has been widely assumed for many behavioral traits, but not so widely demonstrated.

Changes in Fitness Parameters Under Colonization

Life history parameters can exhibit genetic and phenotypic covariance that may be

positive or negative in different environments (Stearns 1989). Negative covariances between life history parameters will constitute an obvious restraint for selection on individual components of fitness. It is clearly not possible in a few generations for selection to increase fitness with respect to every stage in the life cycle and every metabolic activity simultaneously (Dickerson 1955). It is possible, say, that increased fecundity may entail, in the absence of a complete remaking of the reproductive system, a reduction in viability or retarded development. When we consider the results of natural selection in the short term we must assume that only small increases in fitness can be made and that drastic and independent changes cannot be made in all aspects of physiology and morphology (Lewontin 1965).

The inadvertent strong directional selection to decrease the age of first reproduction is recognized among persons involved in mass rearing Mediterranean fruit flies. When they are trying to maintain high quality in a colony (i.e., not selecting away from the "natural" values of fitness parameters), the practice is to collect eggs from 9–11 day old females (Economopoulos et al. 1990) rather than the approximately 3 day old females used in large mass rearing facilities.

The rearing of physiologically and behaviorally competent flies must be a critical priority of all programs using genetic methods to control the Mediterranean fruit fly. Loss of mating competitiveness during mass rearing—for which there is some evidence in the Mediterranean fruit fly—can mean the difference between success and failure of SIT programs (Rössler 1975a,b, 1980). If we are to fully understand the dynamic changes caused by colonization and mass rearing we will need models where many complex factors are incorporated. For example, models built to study selection for courtship and mating behavior under artificial conditions, especially for early and free (i.e., lacking a full complement of courtship signals) mating must be placed in the context of the loss of genetic variation caused by strong inbreeding and its maintenance by heterozygote advantage (Calkins 1989a).

Are Fruit Flies *r* or *K* Selected?

The idea of a continuum of ecological types from *r* (colonizing) selected or *K* (stable) selected species has been modified and elaborated (Southwood 1977) in the 2 decades since it was introduced. For example, the original formulations of *r* and *K* selection did not consider differences in population age-structure or temporal fluctuations in survival rates and fecundities (Charlesworth 1980). We believe that it is more useful to refer to colonizing episodes for any species, that is instances of colonization by some population of the species, rather than speaking of a colonizing species as such. The possibilities for interdeme selection for optimization of reproductive strategies are greatest in species with frequent colonizing episodes (Lewontin 1965)—a fact to remember when we consider models for how natural selection may have operated on tephritid fruit flies in the wild. We have seen above the importance of early sexual maturity for population growth (Cole 1954). From this we might predict that little genetic variance in development time will be found in species with frequent colonizing episodes (high *r*) species, whereas relatively larger amounts of variance for fecundity (with less relative effect on *r*) might be expected in such species (Lewontin 1965). For example, in *Drosophila serrata* Malloch, large differences in fecundity and longevity exist between geographical races, but there are no differences between races in developmental time (Birch et al. 1963). It would certainly be worthwhile to examine mass-reared and wild populations of Mediterranean fruit flies to see how much variation exists for developmental time vis-à-vis variation in fecundity or longevity. There are long standing wild populations in Hawai'i, Guatemala, and Mexico and derived populations in the respective mass rearing facilities. These paired populations

give us the opportunity to compare demographic parameters in populations of the same species that have been subject to different demographic regimes for long periods.

We have evidence for strong directional selection in wild and laboratory populations of fruit flies (Calkins 1989a). For example, in the Mediterranean fruit fly evidence exists for shorter pre-oviposition period (Vargas & Carey 1989), earlier and faster mating, shortened courtship, shortened development time, shorter oviposition period (Wong & Nakahara 1978, Rössler 1975a); and in the Oriental fruit fly for shorter pre-oviposition period (Foote & Carey 1987). These changes appear to be associated with selection for increased growth rate (r) and are not consistent with a model of exhausted variance for developmental time as we would expect in a pure colonizing (r selected) species such as *Drosophila serrata*. Moreover, there is great variation in longevity in Mediterranean fruit fly populations; 50% die within 60 days despite the "best of care" (Back & Pemberton 1918) but others can live up to 7 months.

Until extensive population comparisons are done, we can only speculate that the Mediterranean fruit fly is not an extreme r selected or colonizing species, but is adapted to more stable and predictable environments. Supporting this are observations that indicate that laboratory colonization can change values of certain life history parameters (i.e., shorten development time to sexual maturity) (Wong & Nakahara 1978, Harris et al. 1983), which we would not find in a pure colonizing (r selected) species. For example, in a clearly r selected (colonizing) species, *Drosophila subobscura* Collin, Clarke et al. (1961) observed a strongly asymmetrical response to artificial selection for development time. Realized heritability of *D. subobscura* was 0.06 for downward selection and 0.19 for upward selection. We conclude that wild Mediterranean fruit fly populations still retain variation for shortened development time (which can be exhausted during laboratory colonization), while r selected species like *D. subobscura* exhibit little response to directional selection for decreased development time.

More support for the model of limited colonizing episodes come from descriptions of the natural life history of the Mediterranean fruit fly. The most important factors that determine distribution and abundance of the Mediterranean fruit fly are the succession of host fruits and their availability throughout the year (Bodenheimer 1951). Mediterranean fruit flies can survive temperatures that dip below threshold levels for development for short periods of time. However, even if most of the yearly climate is highly favorable, a lack of available hosts during a period of hot dry weather may make an area unsuitable for sustained colonization (Bodenheimer 1951). The continued presence of Mediterranean fruit fly populations in such an area will then depend on a chance influx of migrants (i.e., a colonizing episode).

We propose that the extreme genetic and phenotypic flexibility of the Mediterranean fruit fly reflects high variability for reproductive strategies within the species. The natural life cycle is adapted to fairly regular and predictable host sequences and low densities, but the occasional episodes necessary for recolonization have maintained genotypes that retain higher r selected life history parameters.

Mating Behavior

Field researchers have observed 2 mating strategies in the Mediterranean fruit fly: 1) males aggregating on leaves to perform courtship rituals; and 2) males approach already mated and ovipositing females on host fruits and attempt to copulate with no prior courtship (Prokopy & Hendrichs 1979, Harris et al. 1988, Hendrichs et al. 1991). There is no evidence to support whether these 2 field mating behaviors represent different subpopulations of males or males that alternate behaviors at different times.

The second strategy is less common in the field with the female usually rejecting the

male (Prokopy & Hendrichs 1979, Burk & Calkins 1983, Hendrichs & Hendrichs 1990). Studies conducted in very different field environments have reported varying figures for the incidence of mating on the host fruit. Prokopy & Hendrichs (1979) reported that, when caged with virgin females, 11% of males were on coffee fruits in field cages in Guatemala. When caged with recently mated females, 23% of males were on fruits. In contrast, Hendrichs & Hendrichs (1990) observed only 1% of mating pairs on fruit in an orchard in Egypt.

In laboratory studies there was a low rate of remating in a control strain (8.4%) even after several hundred generations of rearing under crowded conditions (Saul & McCombs 1993b). This low frequency of remating in the field and laboratory seems inconsistent with the demonstration in laboratory studies that sperm of second mating males predominates in the offspring (Saul et al. 1988, Saul & McCombs 1993a). If there is at least a partial genetic basis for minimal courtship mating on host fruits, then this predominance of offspring from second male maters should have led to an increase in the frequency of remating behavior. On the contrary, this behavior remains rare in the field and laboratory suggesting that there must be some balancing selection against the remating behavior. Predation is a logical choice for this selective force (Hendrichs et al. 1991). In the field, Mediterranean fruit flies are continuous targets of predation by praying mantids, damselflies, vespids, and libellulid dragonflies. In exposed locations like host fruits, the success rate for predation by praying mantids increased to 1 in 4 when females began to oviposit (Hendrichs & Hendrichs 1990).

Evidence that may help to explain this apparent inconsistency comes from recent work on multiple-mated Mediterranean fruit flies (Saul & McCombs 1993a). The mean number of pupae produced by twice-mated females was significantly higher 3–4 weeks after mating than that of once-mated females. Twice-mated females produced a mean of 33 pupae during the period from days 22–30 after mating, while once-mated females produced a mean of 5 pupae during the same period (Saul & McCombs 1993a). This sustained progeny production may provide a clue to the selective advantage of multiple mating in the Mediterranean fruit fly. The major factor determining survival of the Mediterranean fruit fly in the field is the ability of the fertile adult female (there is no larval or pupal diapause in this species) to survive through periods of unfavorable weather or lack of suitable hosts (Back & Pemberton 1918, Bodenheimer 1951). Because twice-mated females have a prolonged period of progeny production, they may be important to the continued survival of the species after periods of environmental stress. We conclude that under most conditions, remating behavior does not increase the fitness of the individual male or female, and indeed may be selected against through increased risk of predation. However, at certain times the female who accepts remating may have an individual selective advantage because of her prolonged fertile egg production. If second matings and sperm mixing should turn out to be present in wild populations, even at relatively low frequencies, it could be significant in the management of SIT programs as well as important to our understanding of the evolution of reproductive strategies in tephritid fruit flies.

The Dangers of Oversimplification in Behavioral Genetics

As illustrated several times above, we may be able in a relatively simple laboratory or field experiment to isolate some ecological or behavioral component that appears to be the cause of an observed pattern in a species. We must be on guard against this natural tendency to oversimplify (Whittier & Kaneshiro 1991). An excellent example comes from the work of Markow & Sawka (1992) with *Drosophila melanogaster* Meigen. In this species there is a complex basis for sexual selection—with important parallels to the situation in tephritids. In a natural breeding/feeding site males and females continually

arrive and depart during an activity period of several hours. Rather than coming from a homogeneous released cohort, males and females vary across a range of genetic and non-genetic characters including size, vigor, fertility, age, and mating status. Their experiments demonstrated that no single male character can be pinpointed that, over time, consistently determines the outcome of sexual selection. They were unable to single out one mechanism (i.e., male competition or female choice) that is consistently responsible for determining the outcome of courtships. Experiments with short observation periods indicated that male courtship vigor was responsible for male success, but experiments with longer observation periods pointed to other factors (Markow & Sawka 1992).

The Role of Models in Ecological Genetics

Levins (1968) described models as the basic units for theoretical investigation, as reconstructions of nature for the purpose of study. There are several distinct roles of models in biological science. One role is the creation of simple plausible explanations for what we know. Because there is an infinitude of explanations for each observation (hence the need for the famous razor of William of Occam), their generation is valuable, but insufficient to determine causation. Models should aid in the identification of relevant and sufficient parameters as new objects of study. Finally and most importantly, models should lead to the fairly direct generation of testable hypotheses (Levins 1968). We must remember that the legitimacy or illegitimacy of a particular model depends on the purpose of the study, and the detailed analysis of a model for purposes other than those for which it was constructed may be meaningless (Levins 1968).

The lek model. One commonly accepted definition of the lek model (Kimsey 1980) has 4 major components: 1) aggregation and display of males at specific sites for mating; 2) male defense of territories from conspecifics; 3) mating territories that do not contain food resources or oviposition sites; and 4) females are able to select their mates. Bradbury (1977) adds some secondary features of the lek model that include strong sexual dimorphism, sexual bimaturism with later maturing males, traditional location of arenas, extreme ritualization of male displays, and highly skewed mating success among males in any given arena. The lek model has often been used to describe any aggregation of territorial males in which mating can occur (Bradbury 1977), but such indiscriminate use of this model can lead to the lumping together of quite different mating strategies.

The intense competition for mates characteristic of those species that have demonstrable lek systems has proved useful in the study of the components of sexual selection (Beehler & Foster 1988) by aiding in the identification of relevant parameters as new objects of study. Unfortunately in tephritid biology, the most important role of the lek model (Prokopy & Hendrichs 1979)—the fairly direct generation of testable hypotheses—has been overshadowed by its use as a rhetorical tool to question the effectiveness of mass rearing technologies. There is no debate that loss of behavioral competence in mass-reared males would have obvious relevance to large scale SIT programs. Moreover, if the lek model is appropriate there would be no debate that behavior related to it would be an important area of research. However, we must first establish the appropriateness of the lek model to the Hawaiian *Ceratitis* Macleay and *Bactrocera*.

Prokopy & Hendrichs (1979) were the first to attempt to apply the lek model to the Mediterranean fruit fly. Their study in Guatemala encompassed several days of observations using a small (1.9 x 1.2 m canopy diameter) coffee tree in a field cage with (tied on) coffee berries and flies collected as pupae from infested coffee and almonds in Costa Rica. Since that paper, many authors have treated the lek model as an assumed starting point rather than a generator of testable hypotheses. For example, Arita & Kaneshiro (1985) proposed a model of a Mediterranean fruit fly lek system that involves competition among

individuals of the same sex and interactions between individuals of the opposite sex. In this system, males select a spot on a leaf and defend it from other males and females sit outside the lek before visiting the "dominant site" and determining with which male she will mate. Their lek model is presented as proven and no reasonable alternate (e.g., random aggregation) models that could account for the observations are proposed or tested.

Another recent example where the lek model is assumed is in the work of Hendrichs & Hendrichs (1990). They observed hundreds of Mediterranean fruit flies on non-host as well as host trees in Egypt [as do Whittier et al. (1992) in Hawaii]. However, this is a condition excluded in Kimsey's (1980) definition of lek. Thirty-seven percent of calling was done by single males while 63% occurred in "leks" (i.e., groups of 2 or more males). In their experimental area, the "leks" were observed to constantly shift position over time. Hendrichs & Hendrichs (1990) did not consider the apparently reasonable alternate hypothesis that they were observing males randomly dispersed on leaves in a region of the trees with favorable light and/or wind conditions. This alternate model proposes that the dispersion pattern of the several hundred males observed calling singly or in groups of 2 or more could fit some underlying random (i.e., Poisson) probability distribution. A similar situation is reported by Iwahashi & Majima (1986) who describe the spatial distribution of calling males of the melon fly, *Bactrocera cucurbitae*, on leaves of *Bidens pilosa* L. in Okinawa as an example of lek behavior. However, their data (Table 1 in their paper) is an excellent fit to a random (Poisson) distribution (Chi-square = 2.407; $P = 0.49$).

Calkins (1989b) believes that an appropriate application of the lek model to tephritids involves the genus, *Anastrepha* Schiner. Host fruits in the tropics for this group are randomly dispersed in time and space and each is only available for short periods of time. Female flies must, therefore, rapidly locate and exploit hosts and then disperse widely to locate other noninfested hosts in other areas. However, in contrast to the definitions of leks presented above, the unpredictability of host distribution and abundance means that males are not able to defend host fruit from other males nor restrict female access to it in exchange for mating opportunities.

We do not dismiss the lek model as inappropriate for all Hawaiian tephritid species. However, we do insist that the reasonable assumptions (Bradbury 1977, Kimsey 1980) be rigorously tested for each species and the model discarded or changed if it is found to be inappropriate rather than distorted to fit the actual observations (Shelly & Kaneshiro 1991, Whittier et al. 1992). The legitimacy of the lek model depends on the purpose of the study, and its detailed analysis for species other than those for which it was constructed (e.g., Hawaiian Drosophilidae) may be meaningless.

At present, we can ask how the lek model, as it has been applied to Hawaiian tephritids, fits the different roles of models as described above. Assuming the observations of male mating and courting behavior are confirmed, is the lek model a plausible explanation for what we observe? We are not convinced that the lek model is appropriate for the Mediterranean fruit fly in Hawaii or most other parts of the species range, and it is even less applicable to the *Bactrocera* species, which lack sexual dimorphism. Moreover, we fail to see that the lek model has identified any relevant parameters as new objects of study. Most importantly, it has not led to the direct generation of testable hypotheses, but has been treated as proven. Current studies of mating aggregations of tephritid fruit flies using systematic and extensive observation and testable alternate hypotheses may help resolve some of the uncertainty outlined above (Sivinski 1990).

CONCLUSIONS

The powerful models and ideas from the areas of genetics, ecology, and ecological genetics can be of immense value to those of us working in insect control. There are sev-

eral steps in the process of incorporating these models and ideas, and the obvious first one is testing their appropriateness and applicability to our systems. Only then can we begin to use these models for the insights they give us into basic biological processes in our organisms as well as for their heuristic value—suggestions for future research directions.

We have chosen the lek model for particular attention since it illustrates the potential power of the models and concepts from ecology and genetics to insect control as well as the problems encountered when the models are prematurely or inappropriately applied. We feel that moving on to the use of the lek model in tephritid biology is still premature because there is no convincing evidence for the first step—the applicability of the model to the species. Scientific testing of the lek model against random or other dispersion pattern models remains to be done.

ACKNOWLEDGMENTS

Journal Series number 4051 of the University of Hawaii Institute of Tropical Agriculture and Human Resources. This research was supported in part by USDA under CSRS Special Grant HAW-00763-G.

LITERATURE CITED

- Arita L.H. & K.Y. Kaneshiro. 1985. The dynamics of the lek system and mating success in males of the Mediterranean fruit fly, *Ceratitis capitata* (Wiedemann). Proc. Hawaii. Entomol. Soc. 25: 39–48.
- Back, E.A. & C.E. Pemberton. 1918. The Mediterranean fruit fly in Hawaii. U.S. Dep. Agric. Bull. 536, 119 p.
- Beehler, B.M. & M.S. Foster. 1988. Hotshots, hotspots, and female preference in the organization of lek mating systems. Am. Nat. 131: 203–19.
- Birch, L.C., T. Dobzhansky, P. Elliott & R.C. Lewontin. 1963. Relative fitness of geographic races of *Drosophila serrata*. Evolution 17: 72–83.
- Bloem, K., S. Bloem, D. Chambers, M. Villatoro & E. Muñiz. 1990. Field evaluation of quality: release-recapture of sterile medflies of different sizes, p. 53 In International Symposium on Fruit Flies of Economic Importance 1990, Antigua Guatemala, Guatemala, October 14–20, 1990. [Abstract.]
- Bodenheimer, F.S. 1951. Citrus entomology of the Middle East, with special reference to Egypt, Iran, Palestine, Syria, Turkey. W. Junk, s'Gravenhage. xii + 663 p.
- Boller, E.F. & C.O. Calkins. 1984. Measuring, monitoring and improving the quality of mass-reared Mediterranean fruit flies, *Ceratitis capitata* Wied. 3. Improvement of quality by selection. Z. Angew. Entomol. 98: 1–15.
- Bradbury, J.W. 1977. Lek mating behavior in the hammer-headed bat. Z. Tierpsychol. 45: 225–55.
- Burk, T. & C.O. Calkins. 1983. Medfly mating behavior and control strategies. Fla. Entomol. 66: 3–18.
- Bush, G.L. & R.W. Neck. 1976. Ecological genetics of the screwworm fly, *Cochliomyia hominivorax* (Diptera: Calliphoridae) and its bearing on the quality control of mass-reared insects. Environ. Entomol. 5: 821–26.
- Calkins, C.O. 1989a. Quality control, p. 153–65. In: Robinson, A. S. & G. H. Hooper, eds., Fruit flies: their biology, natural enemies and control. Elsevier Science Publications, Amsterdam.
- Calkins, C.O. 1989b. Lekking behavior in fruit flies and its implications for quality assessments, p. 135–40. In Cavalloro, R., ed., Proceedings of the International Symposium on Fruit Flies of Economic Importance. Rome. April 7–10, 1987. A. A. Balkema, Rotterdam.

- Chambers, D.L., C.O. Calkins, E.F. Boller, Y. Ito & R.T. Cunningham. 1983. Measuring, monitoring and improving the quality of mass-reared Mediterranean fruit flies, *Ceratitis capitata* Wied. 2. Field tests for confirming and extending laboratory results. *Z. Angew. Entomol.* 95: 285–303.
- Charlesworth, B. 1980. Evolution in age-structured populations. Cambridge University Press, Cambridge.
- Cladera, J.L. 1981. Absence of recombination in the male of *Ceratitis capitata*. *Experientia* 37: 342–43.
- Clarke, J.M., J.M. Smith & K.C. Sondhi. 1961. Asymmetrical response to selection for rate of development in *Drosophila subobscura*. *Genet. Res.* 2: 70–81.
- Cole, L.C. 1954. The population consequences of life history phenomena. *Q. Rev. Biol.* 29: 103–37.
- Dickerson, G.E. 1955. Genetic slippage in response to selection for multiple objectives. Cold Spring Harbor Symp. Quant. Biol. 20: 213–24.
- Economopoulos, A.P., Y. Nitzén & Y. Rössler. 1990. Mass rearing, QC and male-only SIT application with a pupal colour genetic sexing strain of Mediterranean fruit fly. In International Symposium on Fruit Flies of Economic Importance 1990, Antigua Guatemala, Guatemala, October 14–20, 1990. [Unpaginated abstract.]
- Foote, D. & J.R. Carey. 1987. Comparative demography of a laboratory and a wild strain of the Oriental fruit fly, *Dacus dorsalis*. *Entomol. Exp. Appl.* 44: 263–68.
- Foster, G.G., R.H. Maddern & A.T. Mills. 1980. Genetic instability in mass-rearing colonies of a sex-linked translocation strain of *Lucilia cuprina* (Wiedemann) (Diptera: Calliphoridae) during a field trial of genetic control. *Theoret. Appl. Genet.* 58: 169–75.
- Hardy, D.E. & R.H. Footé. 1989. Family Tephritidae, p. 502–31. In Evenhuis, N.L., ed., Catalog of the Diptera of Australian and Oceanian Regions. Bishop Museum Press, Honolulu & E. J. Brill, Leiden.
- Harris, D.J., R.J. Wood & S.E.R. Bailey. 1983. Studies on mating in the Mediterranean fruit fly, *Ceratitis capitata* Wied., p. 197–202. In Cavalloro, R., ed., Fruit flies of economic importance. A. A. Balkema, Rotterdam.
- Harris, D.J., R.J. Wood & S.E.R. Bailey. 1988. Two-way selection for mating activity in the Mediterranean fruit fly, *Ceratitis capitata*. *Entomol. Exp. Appl.* 47: 239–48.
- Hartl D.L. & A.G. Clark. 1989. Principles of Population Genetics. 2nd Ed. Sinauer Assoc., Sunderland, Massachusetts.
- Haymer, D.S., D.O. McInnis & L. Arcangeli. 1992. Genetic variation between strains of the Mediterranean fruit fly, *Ceratitis capitata*, detected by DNA fingerprinting. *Genome* 35: 528–33.
- Hendrichs, J. & M. Hendrichs. 1990. Mediterranean fruit fly (Diptera: Tephritidae) in nature: location and diel pattern of feeding and other activities on fruiting and non-fruiting hosts and nonhosts. *Ann. Entomol. Soc. Am.* 83: 632–41.
- Hendrichs, J., B.I. Katsoyannos, D.R. Papaj & R.J. Prokopy. 1991. Sex differences in movement between natural feeding and mating sites and tradeoffs between food consumption, mating success and predator evasion in Mediterranean fruit flies (Diptera: Tephritidae). *Oecologia* 86: 223–31.
- Huettel, M.D., P.A. Fuerst, T. Maruyama & R. Chakraborty. 1980. Genetic effects of multiple population bottlenecks in the Mediterranean fruit fly (*Ceratitis capitata*). *Genetics* 94s: 47–48. [Abstract.]
- Iwahashi, O. & T. Majima. 1986. Lck formation and male-competition in the melon fly, *Dacus cucurbitae* Coquillett (Diptera: Tephritidae). *Appl. Entomol. Zool.* 21: 70–75.
- Jones, S.R., M.C. Zapater & K.C. Kim. 1993. Morphological adaptation to different

- artificial oviposition substrates in the aculeus of *Ceratitis capitata* (Diptera: Tephritidae). *Ann. Entomol. Soc. Am.* 86: 153–57.
- Kimsey, L.S. 1980. The behaviour of male orchid bees (Apidae, Hymenoptera, Insecta) and the question of leks. *Anim. Behav.* 28: 996–1004.
- Kourti, A., M. Loukas & A. Economopoulos. 1985. Genetic studies in medfly population [unpaginated section]. In Report on Research Co-ordination Meeting on the Development of Sexing Mechanisms in Fruit Flies through Manipulation of Radiation-induced Conditional Lethals and other Genetic Measures, Vienna, Austria, July 15–19, 1985. International Atomic energy Agency/Food and Agriculture Organization of the United Nations, Vienna.
- Leppla, N.C., M.D. Huettel, D.L. Chambers, T.R. Ashley, D.H. Miyashita, T.T.Y. Wong & E.J. Harris. 1983. Strategies for colonization and maintenance of the Mediterranean fruit fly. *Entomol. Exp. Appl.* 33: 89–96.
- Levins, R. 1968. Evolution in changing environments. Princeton University Press, Princeton, New Jersey. ix + 120 p.
- Lewontin, R.C. 1965. Selection for colonizing ability, p. 77–94. In Baker, H., ed., The genetics of colonizing species. Academic Press, New York.
- Livadaris, Y., M. Vasilaki, C. Savakis, A. Malacrida, G. Gasperi & A.S. Robinson. 1990. New mutants in the Mediterranean fruit fly, *Ceratitis capitata*. In International Symposium on Fruit Flies of Economic Importance 1990, Antigua Guatemala, Guatemala, October 14–20, 1990. [Unpaginated abstract.]
- Markow, T.A. & S. Sawka. 1992. Dynamics of mating success in experimental groups of *Drosophila melanogaster* (Diptera: Drosophilidae). *J. Insect Behav.* 5: 375–83.
- Matthews, T.C. & G.B. Craig, Jr. 1989. Isozyme polymorphisms maintained by lethal loci in inbred strains of *Aedes triseriatus*. *J. Hered.* 80: 53–57.
- Mazzioli, J.A. & M.C. Zapater. 1990. Stability of two pupal sexing strains of the Mediterranean fruit fly in mass-rearing colonies. In Laboratory and field evaluation of genetically altered Mediterranean fruit flies for use in sterile insect technique programs, FAO/IAEA Research Coordination meeting, Vienna, Austria, September 24–28, 1990. FAO/IAEA, Vienna, Austria.
- McCombs, S.D. 1992. Genetic studies of the Oriental fruit fly, *Bactrocera dorsalis* (Hendel) (Diptera: Tephritidae): description and linkage analysis of genetic markers. Ph.D. dissertation, University of Hawaii at Manoa, Honolulu.
- McCombs, S.D. & S.H. Saul. 1992a. Linkage analysis of five new genetic markers of the Oriental fruit fly, *Bactrocera dorsalis* (Diptera: Tephritidae). *J. Hered.* 83: 199–203.
- McCombs, S.D. & S.H. Saul. 1992b. Linkage analysis of three new alleles affecting puparium morphology in the Oriental fruit fly, *Bactrocera dorsalis* (Diptera: Tephritidae). *Ann. Entomol. Soc. Am.* 85: 799–804.
- Morgante, J.S., H.M.L. de Souza, E. de Conti & M. Cytrynowicz. 1981. Allozymic variability in an introduced fruit fly pest *Ceratitis capitata* (Wiedemann), 1824, (Diptera-Tephritidae). *Rev. Bras. Genet.* (4) 2: 183–91.
- Mukiyama, T.K. 1985. East African strains of *Ceratitis capitata*: occurrence and enzyme variation. In Report on research co-ordination meeting on the development of sexing mechanisms in fruit flies through manipulation of radiation-induced conditional lethals and other genetic measures, Vienna, Austria, July 15–19, 1985. International Atomic Energy Agency/Food and Agriculture Organization of the United Nations. Vienna.
- Muñiz, M. 1985. Studies on a rapid adaptation of the Mediterranean fruit fly. In Cavalloro, R., ed., Proceedings of the IOBC/WPRS International Symposium on Fruit flies of Economic Importance. Hamburg.

- Papaj, D.R., R.J. Prokopy, P.T. McDonald & T.T.Y. Wong. 1989. Differences in learning between wild and laboratory *Ceratitis capitata* flies. *Entomol. Exp. Appl.* 45: 65–72.
- Prokopy, R.J. & J. Hendrichs. 1979. Mating behavior of *Ceratitis capitata* on a field-caged host tree. *Ann. Entomol. Soc. Am.* 72: 642–48.
- Prokopy R.J., P.T. McDonald & T.T.Y. Wong. 1984. Inter-populational variation among *Ceratitis capitata* flies in host-acceptance pattern. *Entomol. Exp. Appl.* 35: 65–69.
- Riva, M.E. 1990. Stability of a double translocation strain in *C. capitata*, p. 40. *In* International Symposium on Fruit Flies of Economic Importance 1990, Antigua Guatemala, Guatemala, October 14–20, 1990.
- Robinson, A.S. 1984. Unexpected segregation ratios from male-linked translocations in the Mediterranean fruit fly, *Ceratitis capitata* (Diptera: Tephritidae). *Genetica* 62: 209–13.
- Robinson, A.S. & C. van Heemert. 1982. *Ceratitis capitata*—a suitable case for genetic sexing. *Genetica* 58: 229–37.
- Rössler, Y. 1975a. Reproductive differences between laboratory-reared and field-collected populations of the Mediterranean fruit fly, *Ceratitis capitata*. *Ann. Entomol. Soc. Am.* 68: 987–91.
- Rössler, Y. 1975b. The ability to inseminate: a comparison between laboratory-reared and field populations of the Mediterranean fruit fly, *Ceratitis capitata*. *Entomol. Exp. Appl.* 18: 255–60.
- Rössler, Y. 1980. Sexual competitiveness of males of the Mediterranean fruit fly, *Ceratitis capitata* (Wiedemann) (Diptera: Tephritidae), carrying a Y-chromosome translocation. *Bull. Entomol. Res.* 70: 649–56.
- Rössler, Y. 1982. Recombination in males and females of the Mediterranean fruit fly (Diptera: Tephritidae) with and without chromosomal aberrations. *Ann. Entomol. Soc. Am.* 75: 619–22.
- Rössler, Y. 1985. Effect of genetic recombination in males of the Mediterranean fruit fly (Diptera: Tephritidae) on the integrity of “genetic sexing” strains produced for sterile insect releases. *Ann. Entomol. Soc. Am.* 78: 265–70.
- Saul, S.H. 1989. Genetics of the Mediterranean fruit fly (*Ceratitis capitata*) (Wiedemann), p. 1–36. *In* Russell, G.E., ed., *Genetical and biochemical aspects of invertebrate crop pests*. Intercept Ltd., Andover, Hampshire, UK.
- Saul, S.H. 1990. A genetic sexing system to improve the sterile insect technique against the Mediterranean fruit fly. *J. Hered.* 81: 75–78.
- Saul, S.H. & S.D. McCombs. 1993a. Dynamics of sperm use in the Mediterranean fruit fly (Diptera: Tephritidae): reproductive fitness of multiple mated females and sequentially mated males. *Ann. Entomol. Soc. Am.* 86: 198–202.
- Saul, S.H. & S.D. McCombs. 1993b. Increased remating frequency in sex distorted lines of the Mediterranean fruit fly. *Ann. Entomol. Soc. Am.* 86: 631–37.
- Saul, S.H., S.Y.T. Tam & D.O. McInnis. 1988. Relationship between sperm competition and copulation duration in the Mediterranean fruit fly (Diptera: Tephritidae). *Ann. Entomol. Soc. Am.* 81: 498–502.
- Sharp, J.L., E.F. Boller & D.L. Chambers. 1983. Selection for flight propensity of laboratory and wild strains of *Anastrepha suspensa* and *Ceratitis capitata* (Diptera: Tephritidae). *J. Econ. Entomol.* 76: 302–05.
- Shelly, T. & K.Y. Kaneshiro. 1991. Lek behavior of the Oriental fruit fly, *Dacus dorsalis*, in Hawaii (Diptera: Tephritidae). *J. Insect Behav.* 4: 235–41.
- Sheppard, W.S., G.J. Steck & B.A. McPheron. 1992. Geographic populations of the

- medfly may be differentiated by mitochondrial DNA variation. *Experientia* 48: 1010–1013.
- Sivinski, J. 1990. Tephritid sexual behavior, p. 48. *In* International Symposium on Fruit Flies of Economic Importance 1990, Antigua Guatemala, Guatemala, October 14–20, 1990.
- Southwood, T.R.E. 1977. Habitat, the templet for ecological strategies? *J. Anim. Ecol.* 46: 337–65.
- Stearns, S.C. 1989. The evolutionary significance of phenotypic plasticity. *BioSci.* 39: 436–45.
- Stearns, S.C. & J.C. Koella. 1986. The evolution of phenotypic plasticity in life-history traits: predictions of reaction norms for age and size at maturity. *Evolution* 40: 893–913.
- Tanaka, N. 1965. Artificial eggging receptacles for three species of fruit flies. *J. Econ. Entomol.* 58: 177–78.
- Vargas, R.I. 1984. Alternative egg collection system for mass production of Mediterranean fruit fly (Diptera: Tephritidae). *J. Econ. Entomol.* 77: 1064–1069.
- Vargas, R.I. & J.R. Carey. 1989. Comparison of demographic parameters for wild and laboratory-adapted Mediterranean fruit fly (Diptera: Tephritidae). *Ann. Entomol. Soc. Am.* 82: 55–59.
- White, I.M. & M.M. Elson-Harris. 1992. Fruit flies of economic significance; their identification and bionomics. CAB International Institute of Entomology, Wallingford, UK. xii + 601 p.
- Whitten, M.J. 1979. The use of genetically-selected strains for pest replacement or suppression, p. 31–40. *In* Hoy, M. A. & J. J. McKelvey, Jr., eds., Genetics in relation to insect management, working papers of the Rockefeller Foundation. Rockefeller Foundation, New York.
- Whittier, T.S. & K.Y. Kaneshiro. 1991. Male mating success and female fitness in the Mediterranean fruit fly (Diptera: Tephritidae). *Ann. Entomol. Soc. Am.* 84: 608–11.
- Whittier, T.S., K.Y. Kaneshiro & L.D. Prescott. 1992. Mating behavior of Mediterranean fruit flies (Diptera: Tephritidae) in a natural environment. *Ann. Entomol. Soc. Am.* 85: 214–18.
- Wong, T.T.Y. & L.M. Nakahara. 1978. Sexual development and mating response of laboratory-reared and native Mediterranean fruit flies. *Ann. Entomol. Soc. Am.* 71: 592–96.